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Conference paper

ACROSS SPECIES COMPARISONS IN SELECTION FOR EFFICIENCY

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Summary

Direct selection on feed efficiency is unlikely to be an appropriate method for genetic improvement. Selection on a single trait correlated with feed efficiency would not result in a greater response than direct selection on feed efficiency. Therefore, the main route for genetic improvement in feed efficiency will be through indirect selection on several traits. There is little theoretical advantage from including food intake in the selection criteria for genetic improvement of feed efficiency in dairy and beef cattle, sheep and pigs. Based on experiments, selection for rate of lean growth is preferable to selection for efficiency of lean growth, so it is not necessary to measure food intake. A between-species comparison of selection strategies, which result in genetic improvement of feed efficiency, indicate that a constraint on nutritional inputs may be preferable to selection with ad-libitum feeding. Information is required on genotype with nutrition interactions for milk and carcass composition, meat/eating quality and reproduction traits, for comprehensive evaluation of alternative selection objectives and selection criteria to improve efficiency of production.

Keywords: feed efficiency, genetic improvement, nutrition, selection strategies.

Introduction

An objective of breeding programmes is to increase efficiency of production and irrespective of how efficiency is defined, the efficiency of nutrient utilisation will form a major component of the breeding programme objective. In the pork and the milk production enterprises, feed can account for 70% and 80% of total costs (Meat and Livestock Commission, 1997; Milk Marketing Board, 1990). In pig breeding programmes, feed efficiency, or its

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inverse food conversion ratio, has been incorporated in selection objectives and selection criteria (de Vries and Kanis, 1994). In dairy cattle breeding programmes, selection objectives and criteria have generally focused on outputs, which have not included feed efficiency (Persaud et al., 1991). Measurement of food intake in progeny testing schemes in dairy cattle is not practical, but the introduction of nucleus breeding schemes in dairy cattle has enabled recording of food intake, such that feed efficiency can be included in the selection criterion. In beef cattle and sheep breeding programmes, outputs rather than inputs have also featured in selection criteria (Banks 1994; Barwick et al., 1994), due to the difficulty in recording inputs. However, as with dairy cattle, establishment of nucleus breeding herds in beef cattle and sheep present the opportunity to include feed efficiency in selection objectives and corresponding selection criteria.

The paper focuses primarily on approaches taken or which can be taken for genetic improvement of feed efficiency in dairy and beef cattle, sheep and pigs, and the consequences of selection for feed efficiency.

Direct selection for feed efficiency

Only two pig studies have selected directly on feed efficiency (Jungst et al., 1981; Webb and King, 1983), with pigs penned individually or in groups. In beef cattle, there was only one study with selection on food conversion ratio, the inverse of feed efficiency (Bishop et al., 1991). In the pig studies, responses to several generations of selection were insignificant. Possible reasons for the low responses are, respectively, selection only on males combined with a low heritability of 0.12 and selection primarily on a between-pen basis. In the beef cattle study, selection on males was repeated in the "parental" generation and individual food intake of progeny from selected bulls was not measured. The replicated responses in half sib food conversion ratio were small, possibly due to the adjustment of food conversion ratio for perceived variation in maintenance requirements, such that selection differentials were reduced. The three studies indicate that a significant response to direct selection on feed efficiency requires selection in both males and females and the measurement of individual food intake.

Electronic tagging and the use of electronic feeders in dairy cattle, beef cattle and pigs provide the facility to measure individual food intake, without incurring substantial staff time, but the high equipment costs prohibit both widespread use and continuous measurement of all animals available for selection. Therefore, direct selection on feed efficiency is unlikely to be an appropriate method for genetic improvement.

Indirect selection for feed efficiency

Indirect selection for feed efficiency may be more effective than direct selection. If a trait with heritability, h^2_x, has a genetic correlation r_A with feed efficiency, then the ratio of indirect to direct response in feed efficiency is $r_A h_X / h_{FE}$ per unit selection differential, where h^2_{FE} is the heritability of feed efficiency. Clearly, if the genetic correlation and the heritability of the correlated trait are high, then the response in feed efficiency with indirect selection will be greater than the response with direct selection. For example, given a heritability of 0.20 for feed efficiency, a correlated trait with a genetic correlation of 0.5 or 0.6, in magnitude, would require a heritability of at least 0.80 or 0.56 to have a greater response in feed efficiency than direct selection, per unit selection differential. However, there are few traits which have both a sufficiently high heritability and high genetic correlation with feed efficiency! For example, when food intake was recorded, genetic correlations for food conversion ratio, the inverse of feed efficiency, with growth in beef cattle and pigs were -0.51 and -0.52 (Bishop, 1992; Cameron and Curran, 1994b) and genetic correlations for feed efficiency with milk yield or fat and protein yield were 0.60 and 0.61 (Persaud et al., 1991). However, heritabilities for growth in beef cattle and pigs were 0,37 (Bishop, 1992; Cameron and Curran, 1994b) and were 0.20 and 0.15 for milk yield or fat and protein yield in dairy cattle (Persaud et al. 1991). Although, the genetic correlations were of the "required" order of magnitude, the heritabilities of the correlated traits were too low. Therefore, selection on a single trait correlated with feed efficiency is unlikely to result in a greater response than direct selection on feed efficiency, per unit selection differential.

Although, selection on one correlated trait is theoretically less efficient than direct selection, it should still be possible to identify a single trait or a combination of traits on which to select, such that the correlated response in feed efficiency is maximised. Weight gain, or growth rate, is an obvious trait to consider for indirect selection to improve feed efficiency (= weight gain/food intake), in beef cattle, sheep and pigs. However, few selection experiments in beef cattle or sheep have recorded feed intake, such that there is a lack of information on realised responses in feed efficiency. Of the experiments in which food intake was measured, unidirectional selection for post-weaning growth in cattle increased growth and food intake, but feed efficiency was not reduced, relative to a control line (Irgang et al., 1985). Similarly, divergent selection for weaning weight in sheep did not change feed efficiency (Thompson et al., 1985; Herd et al., 1993). Despite the high emphasis on feed costs in pig production, many selection experiments in pigs have not recorded food intake (e.g. Fredeen and Mikami 1986). However, divergent selection on a growth rate alone resulted in increased growth and food intake, but feed efficiency was not unequivocally improved (Woltman et al., 1992). Responses to selection on growth in beef cattle and pigs suggest that there is little genetic variation in food intake, that is independent of genetic variation in growth, such that feed efficiency is not improved by selection on growth.

A corresponding "output" trait to weight gain in beef cattle, sheep and pigs is milk yield in dairy cattle. There have been few selection studies in ad-libitum fed dairy cattle, with food intake not restricted to be dependent on milk yield. Selection for fat and protein yield in dairy cattle with ad-libitum feeding resulted in increased milk yield, with no change in food intake or in fat and protein content of milk, such that both feed efficiency and energetic efficiency were increased (Veerkamp et al., 1994). The response to selection for fat and protein yield in dairy cattle suggests that there is little genetic variation in feed efficiency that is independent of genetic variation in fat and protein yield. The between-species comparison of the response in feed efficiency with selection on a "simple autput" trait implies a different relationship between food intake and feed efficiency in dairy cattle compared to beef cattle and pigs.

Rather than assessing one aspect of production, it is important that a holistic perspective is taken when evaluating particular selection strategies (Simm et al., 1994; Greeff et al., 1995). Selection for high fat and protein yield resulted in reduced body condition score of heifers, by week 26 of lactation (Veerkamp et al., 1994). If fat and protein yield is positively associated with tissue mobilisation, reflected by lower condition score, then subsequent lactation, reproductive performance (McGowan et al., 1996) and disease status may be adversely affected. Therefore, the framework for a between-species comparison of responses in feed efficiency in dairy cattle, beef cattle, sheep and pigs should take appropriate account of changes in "outputs" as well as changes in food intake. Based on the selection experiments, the "output" in dairy cattle differs from the "output" in beef cattle and pigs, in that the change in body lipid of dairy cattle is contributing to the "output", while the change in body lipid forms part of the "output" in beef cattle, sheep and pigs. Rather than attempting to resolve the energetic contribution of changes in body lipid content to milk yield, there may be another approach.

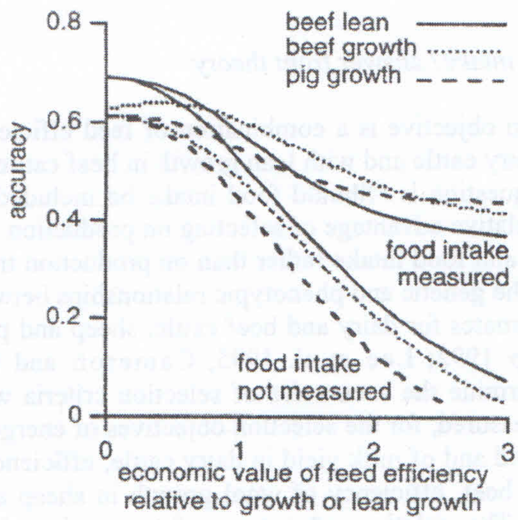
In terms of the response in feed efficiency, selection for lean growth in beef cattle, sheep and pigs may be more consistent with selection for fat and protein yield in dairy cattle, than selection solely for growth. In beef cattle, selection for lean growth, on the basis of growth rate and ultrasonic backfat depth, resulted in increased growth rate and food efficiency, as there was no change in food intake (Mrode et al.,1990b). There are no reports of the response in feed efficiency to selection for lean growth in sheep. In pigs, selection for lean growth with ad libitum feeding, again on the basis of growth rate and ultrasonic backfat depth, has increased growth and feed efficiency, with no change in feed intake (Vangen, 1979, 1980; Cameron and Curran, 1994b). The qualitatively similar responses in food intake and feed efficiency to selection on fat and protein yield in dairy cattle and on lean growth in beef cattle and pigs, suggest that selection strategies of fat and protein yield and for lean growth can be considered as analogous, for the purpose of a between-species comparison of genetic improvement in feed efficiency.

Measure food intake? answer from theory

If the selection objective is a combination of feed efficiency with fat and protein yield in dairy cattle and with lean growth in beef cattle, sheep and pigs, then an obvious question is "Should food intake be included in the selection criterion?". The relative advantage of selecting on production traits, such as fat and protein yield, and food intake rather than on production traits alone can be determined from the genetic and phenotypic relationships between traits.

Parameter estimates for dairy and beef cattle, sheep and pigs (Persaud et al., 1991; Bishop 1992; Lee et al. 1995; Cameron and Curran, 1994b) were used to determine the accuracies of selection criteria when food intake was or was not measured, for the selection objectives of energetic efficiency of fat and protein yield and of milk yield in dairy cattle, efficiency of growth and of lean growth in beef, efficiency of wool growth in sheep and efficiency of growth in pigs. The relative advantage of measuring food intake was essentially zero for dairy cattle, as the genetic correlation between efficiency and food intake was only -0.05 (Persaud et al., 1991). Similarly, with sheep, there was little advantage in recording food intake. For beef cattle and pigs, the accuracy was less sensitive to differences in economic values of feed efficiency and growth rate when food intake was included in the selection criterion, than when food intake was not measured (Figure 1). The benefit from including food intake in the selection criterion, as assessed by the increase in accuracy, was dependent on the economic value per phenotypic standard deviation of feed efficiency relative to that for growth or lean growth. For example in pigs, if growth rate and feed efficiency are worth £0.03 per g/day and £45.00 per kg/kg, with phenotypic standard deviations of 100 and 0.045, then the economic value of one phenotypic standard deviation of feed efficiency, relative to that for growth is 0.68, such that there is little advantage of including food intake in the selection criterion. In beef cattle, a ratio of economic values for feed efficiency and growth rate of unity indicates a marginal advantage in measuring food intake, as confirmed by Simm et al., (1986), when the accuracies of selection criteria with growth rate replaced by feed efficiency were the same. Therefore, genetic improvement of feed efficiency in dairy and beef cattle, sheep and pigs is unlikely to require inclusion of food intake in the selection criteria.

Figure 1. - ACCURACY OF PREDICTED GENETIC MERIT WHEN FOOD INTAKE IS OR IS NOT MEASURED



Measure food intake? answer based on experiments

Only two selection experiments have included selection objectives which did or did not directly include feed efficiency. In the beef selection experiment (Mrode et al., 1990a), the two strategies were rate of lean growth and lean food conversion ratio (= daily food intake/lean growth rate). In the pig selection experiment (Cameron, 1994), one selection objective was designed to achieve equal correlated responses in growth rate and carcass lean, LGA, measured in phenotypic standard deviations, and another selection objective was to achieve equal, but opposite, correlated responses in food conversion ratio and carcass lean, LFC. Although, the beef cattle and pig selection objectives were of a multiplicative and additive nature, respectively, the responses were qualitatively similar. Within each study, the increase in carcass lean and reduction in food conversion ratio with selection for lean growth were similar to the responses with selection for lean food conversion ratio (Mrode et al., 1990b; Cameron and Curran, 1994b, 1995b). In both studies, growth rate was increased with selection for lean growth, but not with selection for lean food conversion. Therefore, in terms of genetic improvement in feed efficiency and growth rate, selection for lean growth or LGA is preferable to selection for lean food conversion ratio or LFC, such that it is not necessary to measure food intake.

Food intake in pigs was reduced with selection for LFC, but not altered with selection for LGA. In beef cattle, selection for lean growth and lean food conversion ratio resulted in increased and reduced food intake, respectively, although the responses were not significant. The different magnitudes of response in food intake in the pig and beef cattle selection experiments may have been a function of the selection differentials, as there were four generations of divergent selection in the pig study and 1.6 generations of uni-directional selection in the beef cattle experiment. However, in both studies, the estimated genetic correlation for food intake with lean food conversion ratio or LFC was higher in magnitude than with rate of lean growth or LGA (0.57 and 0.04 for beef cattle (Mrode et al., 1990b); -0.45 and 0.23 in pigs (Cameron, 1994). A negative correlation is expected in the pig study, as the LFC selection objective had a negative weight on food conversion ratio. The responses to selection and genetic correlation estimates indicate that selection for lean food conversion ratio or LFC in beef cattle and pigs will reduce food intake, which may be acceptable in the short term, but not in the long term, since reproductive performance is consequently reduced (Kerr and Cameron, 1996).

Implicit selection for feed efficiency

The alternative strategy for genetic improvement of feed efficiency (= weight gain/food intake) is to increase the numerator of feed efficiency, rather than reduce the denominator. Increased weight gain per unit of food implies a change in the composition of weight gain. Although the energy required to deposit a unit of protein and lipid are essentially the same, a unit of lean growth requires less energy than a unit of fat growth (Webster, 1977), as the water content of lean tissue is greater than the water content of fat tissue. Therefore, feed efficiency can be improved through increased rate of lean growth with no change in fat growth rate, or *vice versa*, or by the combination of increased lean growth rate and reduced fat growth rate.

In the pig selection experiment (Cameron and Curran, 1995b), the increase in carcass lean with selection on LGA was due to a higher rate of lean growth, as the rate of fat growth was unchanged. In contrast, selection on LFC reduced the rate of fat growth, with no change in rate of lean growth. Responses in carcass composition were not reported in the beef cattle selection study (Mrode et al., 1990a, b). Therefore, selection objectives emphasising rate or efficiency of lean growth present two alternatives to improve feed efficiency. However, to maximise the rate of genetic improvement in feed efficiency, per unit selection differential, a selection objective which results in both increased lean growth and reduced fat growth is required.

The short term response of selection for fat and protein yield in dairy cattle or lean growth in beef cattle and pigs increased efficiency through increasing milk yield or lean growth, without changing food intake (Veerkamp et al., 1994; Mrode et al., 1990b; Vangen, 1979, 1980; Cameron and Curran, 1994b). If genetic improvement in fat and protein yield or lean growth is to be sustained in the long term, then ad-libitum food intake will need to increase, once an acceptable level of lipid mobilisation or carcass fat content, respectively, is achieved. The definition of an "acceptable level of lipid mobilisation" will have to account for the genetic relationships with subsequent performance, in terms of reproduction and lactation. Similarly, in beef cattle, sheep and pigs, an "appropriate carcass fat content" will depend on relationships between carcass fat and meat/eating quality in commercial stock and reproductive performance in breeding animals. In the short term, selection for fat and protein yield or lean growth with a constraint on food intake, will implicitly emphasise feed efficiency (Fowler et al., 1976). No expression of genetic merit in "appetite" would be possible, but then selection for lean growth in beef cattle and pigs did not change ad-libitum food intake in the short term. If ad-libitum food intake increases in the long term, then imposition of a "constant" restriction on food intake, for selection purposes, will require information on the genetic merit for ad-libitum intake, which can be obtained from the ad-libitum food intake of relatives, either from performance test in the previous generation or simultaneously using electronic feeders.

Selection on restricted food intake : genotype with nutrition interaction ?

In pigs, selection for lean growth with a constraint on food intake is preferable, in terms of performance test traits, to selection on ad-libitum feeding, when progeny were reared on ad-libitum feeding regime (Fowler and Ensminger, 1960; McPhee et al., 1988; Cameron and Curran, 1995a).

However, genotype with ration and genotype with diet interactions for growth rate, but not for ultrasonic backfat depth have been demonstrated (Cameron and Curran, 1995a; Bereskin et al., 1990). If there are not corresponding genotype with nutrition interactions for carcass traits, then the perceived advantage of selection for lean growth with a constraint on food intake will be diminished. The lack of an interaction between genotype and nutrition for ultrasonic backfat depth is not necessarily indicative of no interaction for carcass composition (Woltmann et al., 1992). Information on the interaction between genotype with nutrition for meat quality and reproduction traits is required for evaluation of selection criteria. Although, there have been several studies examining genotype (breed) with nutrition interactions (e.g. Quiniou et al., 1996), then as reasons for between-genotype differences are not known, such studies can only provide limited information on the choice of selection strategies.

If the nutritional environments for testing animals and rearing their commercial progeny are substantially different, then the achieved responses will be lower than predicted responses, if no account is taken of the genotype with nutrition interaction. For example, coheritabilities for the selection criteria, with an intensive environment, and performance traits of extensively reared offspring were at most 0.25 in beef cattle (Bishop, 1993) and sheep (Cameron, 1992; Lewis et al., 1996). Foı heritabilities of carcass lean and the selection criteria of 0.4, the genetic correlation between environments of at most 0.6 is indicative of a genotype with nutrition interaction. Use of intensive performance test environments may be less effective than progeny testing in beef cattle and sheep, despite the reduction in generation interval ?

Measurement of food intake is not necessary for genetic improvement in feed efficiency, but food intake is recorded by electronic feeders in nucleus pig herds. Electronic feeders enable testing of animals in a group-pen environment, to mimic a commercial environment and reduce the genotype with nutrition interaction, but still measure individual food intake (Hall et al., 1997). If electronic feeders depress food intake, relative to individually penned animals, such that performance is reduced (de Haer and de Vries, 1993), then the predicted genetic merit of animals tested on electronic feeders will negatively biased. Therefore, if food intake of all animals available for selection cannot be measured, due to a limitation on the number of electronic feeders, then animals not tested on electronic feeders may be preferentially selected. Therefore, use of electronic feeders may introduce another form of genotype with nutrition interaction, which will reduce the perceived advantage of recording food intake.

Conclusion

A between-species comparison of selection strategies resulting in genetic improvement of feed efficiency indicates that inclusion of food intake in selection criterion is not necessary and, in breeding programmes, animals should be performance tested with a constraint on food intake.

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USPOREDBE U SELEKCIJI NA DJELOTVORNOST KROZ VRSTE

Sažetak

Nije vjerojatno da će izravna selekcija na djelotvornost hrane biti odgovarajuća metoda za genetsko poboljšanje. Selekcija na jednu jedinu osobinu u korelaciji s djelotvornosti ne bi dala veći odgovor/reakciju od izravne selekcije na djelotvornost hrane. Stoga će glavni način za genetsko poboljšanje djelotvornosti hrane biti kroz neizravnu selekciju na nekoliko osobina. Mala je teoretska korist od uključivanja unosa hrane u kriterije selekcije za genetsko poboljšanje djelotvornosti hrane u mliječnih i mesnih goveda, ovaca i svinja. Na osnovi pokusa selekcija na stopu mršavog rasta je u prednosti pred selekcijim na djelotvornost mršavog rasta, pa nije potrebno mjeriti unos hrane. Usporedba strategija selekcije među vrstama što dovode do genetskog poboljšanja djelotvornosti hrane pokazuju da ograničenje hranidbenih unosa može biti poželjnije od selekcije s hranjenjem ad libitum. Potrebni su podaci o genotipu s hranidbenim interakcijama za sastav mlijeka i trupa, kakvoće mesa/jedenja i osobine reprodukcije za temeljitu ocjenu ciljeva alternativne selekcije i kriterija selekcije radi poboljšanja djelotvornosti proizvodnje.

Ključne riječi: djelotvornost hrane, genetsko poboljšanje, hranidba, strategija selekcije

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